PROJECT COYOTE

F O S T E R I N G   C O E X I S T E N C E

Dear Interested Person or Party:

The following is a scientific opinion letter requested by Camilla Fox, Executive Director of Project Coyote. This letter outlines a response to the general question "What effect does reduction of coyotes (older than 6 months) have on the remaining population?" This question is central to the repeated claim that reduction (mortality) of adult coyotes from human control practices lessens predation on domestic sheep or game animals such as mule deer or antelope. Before I cover the three basic biological responses by coyote populations to reduction (described below), it is important to understand the type of "predator reduction" or "coyote control" in question. Most reduction programs, often referred to as control practices, are indiscriminate in nature, meaning the individuals removed (coyotes are killed not relocated) are probably not the offending individuals. Research (mostly funded and conducted by USDA Wildlife Services) has shown that offending individuals are most often breeding adults provisioning their pups. Breeding adult coyotes are very difficult to target and can be rapidly replaced (another pack member takes over their role). Even if some offending individuals are removed, there is great likelihood that the responses described below will take place anyway. Although removal of offending individuals may temporarily alleviate predation rates on the protected species, the alleviation is usually short-term and has long-term side-effects that can result in increased predation rates and increasingly ineffective control activities.

It cannot be over-emphasized how powerfully coyote populations compensate for population reductions. Such density dependent responses to exploitation (human-caused mortality) are common in mammals and present in all territorial populations at or near habitat saturation. Both evolutionary biology and the results of research (e.g., recently completed 20 year study in Yellowstone National Park before and after gray wolf reintroduction) indicate that the basis of their *demographic and behavioral* resiliency is embedded in their evolutionary history. Coyotes evolved, and learned to coexist, in the presence of gray wolves—a dominant competitor and natural enemy that overlapped the historic range of coyotes in North America. Prior to widespread human persecution starting in the mid-nineteenth century, wolves have provided a constant selection factor inflicting mortality, competition, and numerous other sub-lethal effects.

Collectively, these intense selective pressures by wolves resulted in a species that exists in a relatively constant state of colonization with many specialized adaptations. These demographic and behavioral adaptations are numerous and diverse and allow coyote populations to easily overcome the relatively mild effects of human control practices which are short-term and intermittent compared to sustained presence of wolves, from every month to many thousands of years.

Demographic compensation

The following demographic responses are based on published research, results of preliminary analysis of coyote study populations subjected to various levels of reduction or exploitation, and the work I have conducted with coyote populations in three study areas over the past 28 years in Washington (an unexploited population, not subject to human control or mortality), California (exploited), and Wyoming (unexploited then wolf mortality after reintroduction).

There is little, if any, scientific basis to justify control (reduction) programs that indiscriminately target adult coyotes. Wildlife Services often points out the lack of academic research demonstrating effectiveness. However, as with any federal action, the burden of proof is upon them to demonstrate both the biological and economical effectiveness of their proposed control activities. In fact, the mechanisms described below suggest that widespread control (even selective control) increases immigration, reproduction, and survival of remaining coyotes. It has been reported that sustained reduction of coyote numbers can only be accomplished if over 70% of the individuals are removed (exploited) on a sustained basis. Review of field research and modeling exercises (including my own) indicates that even with intensive control efforts, this level is rarely, if ever, achieved. A thorough review and synthesis of coyote ecology and demography can be found in a recent book chapter (see Crabtree and Sheldon 1999).

(1) Actual reduction in the density (and number of coyotes) does occur and is primarily a function of lower pack size for one year (betas, yearlings, and 6 month old pups are killed more often than reproducing adults or alphas). However, this reduction is compensated for in a wide variety of ways. First off, immediate immigration occurs in the reduction area by lone animals or from spatial shifts by surrounding social groups. At exploitation rates below 70%, the reproducing alpha males and females are replaced (seldom in the same year but always in the succeeding year). This is the expected response by most territorial species with surplus (non-breeding) adults. Their primary objective is to find a temporal opening, defend and exploit the food resources in that social group, pair-bond and breed.

(2) Human control resulting in density reduction results in a smaller social group size which increases the food per coyote ratio within the territory. The food or prey surplus is biologically transformed into somewhat larger litter sizes and almost always much higher litter survival rates (which are low in unexploited populations). Review of literature indicates that the increase in litter size at birth is not as great as was previously reported by Knowlton (1972). In addition to increased food availability for fast-growing pups, the surplus food improves the nutritional condition of breeding and associate adults, which translates in higher pup birth weights and higher pup survival. Alpha male coyotes and associate adults in the pack help feed the pups.

(3) Density reduction allows the pups that normally die during the summer months in populations with low to no mortality, to survive. Exploitation causing higher pup survival is fundamentally a function of the general mammalian reproductive strategy that delays the majority of reproductive energetic investment beyond the gestation period, the post-partum and neonate state (e.g., young pups). The caloric demand of offspring reaches an apex in May, June, and July when coyote pups grow very fast. Thus, the normal litter of six pups has a good chance of (a) surviving the typically high summer mortality period and, (b) being recruited into the pack

the following winter as adults thereby returning the previously exploited population to normal densities. By contrast, in the two unexploited populations I investigated, the average litter size at birth was 5 or 6, but due to high summer mortality, only an average of 1.5 to 2.5 pups survive. In populations subjected to less than 70% removal annually, there appears to be an ample number of breeding pairs to occupy all available territory openings and litter sizes of 6 to 8 enjoy high survival rates (most pups born survive to adulthood). This results in a doubling or tripling of the number of hungry pups that need to be fed. "Large packages" of prey, (such as sheep, as opposed to the more natural and common prey species of voles, mice, or rabbits) make for more efficient sources of nutrition because hunting adults have to invest less energy per unit of food obtained. Research funded by Wildlife Services clearly indicates that the primary motivation to kill domestic sheep is to provide food for fast-growing pups.

(4) Reductions in coyotes capable of breeding (at 10 months of age) result in smaller pack size which leaves fewer adults to feed pups. This may further add incentive for the remaining adults to kill larger prey as well as putting pressure on the adults to select for the most vulnerable prey and venture close to areas of human activity. Because predators like coyotes also learn what is appropriate food when they are pups, and are reluctant to try 'new' food sources unless under stress (such as having to feed a large litter of pups), reduction programs, in effect, may be forcing coyotes to try new behaviors (eating domestic livestock) which they would otherwise avoid. Research has clearly shown that higher numbers of adult pack members provide more den-guarding time and more food brought to pups. Without pressure to "maximize" efficiency in hunting for food for pups, packs may be able to subsist on larger numbers of smaller prey (e.g., rabbits and small rodents) rather than going for livestock or other, larger prey like antelope and mule deer fawns. Although, coyotes are exposed to significant risk of injury when hunting and killing larger prey, larger litter sizes might 'tip the balance' in favor of selecting larger prey and livestock.

(5) Reductions (non-selective, indiscriminate killing of adults) cause an increase in the percentage of females breeding. Coyote populations are distinctly structured in non-overlapping but contiguous territorial packs. About 95% of the time, only one female (the dominant or alpha) in a pack breeds. Other females, physiologically capable of breeding, are "behaviorally sterile". Exploitation rates of 70% or higher are needed to decrease the number of females breeding in a given area. Either a subordinate female pack member, or an outside, lone female can be quickly recruited to become an alpha or breeding female. My research has shown that light to moderate levels of reduction can cause a slight increase in the number of territories, and hence the number of females breeding.

(6) Reduction or removal of coyotes causes the coyote population structure to be maintained in a colonizing state. For example, the average age of a breeding adult in an unexploited population is 4 years old. By age 6, reproduction begins to decline whereby older, alpha pairs maintain territories but fail to reproduce. This may eliminate the need to kill sheep or fawns in the early summer in order to feed pups. Exploiting or consistently reducing coyote populations keeps the age structure skewed to the younger more productive adults (average age of an alpha is 1 or 2 years). Therefore, the natural limitations seen in older-aged, unexploited populations are absent and the territorial, younger populations produce more pups.

(7) Reductions in adult density of coyotes also cause young adults (otherwise prone to dispersing) to stay and secure breeding positions in the exploited area. This phenomenon is well-

documented by research conducted by Wildlife Services and other researchers. Research also indicates that this is the age class most frequently involved in conflicts.

Alternate prey

An aspect of coyote predation on livestock that is often overlooked is the availability, or dearth of alternate prey. Wildlife Services' research has demonstrated that coyotes will avoid novel prey, such as domestic livestock. In addition, it is risky for coyotes to predate upon domestic livestock because of human control actions associated with this behavior. Related research indicates that predators switch to alternative prey when a preferred prey item is absent or in low numbers. Voles and other rodents like jackrabbits are a preferred major staple of coyotes in the West. These prey species require cover and ample supplies of forage (grass and forbs). On many western rangelands grasses, forbs, and protective cover have been greatly reduced by domestic livestock grazing, leaving predators with fewer preferred prey to utilize. Present or historic grazing impacts should be assessed as a likely means of predicting overall predation rates on other prey species, especially prey like domestic sheep, which are already vulnerable to predators due to their lack of anti-predator behaviors.

Accelerated selection pressures and learned behaviors

A relatively unexplored, but promising avenue of research is the long-term genetic and behavioral changes in coyote populations subjected to decades of exploitation. It seems obvious that the type of selection pressures and selection rates have been greatly changed for coyote populations, after a century of exploitation at 20% to 70% per year. More nocturnal, more wary, more productive, more resilient individuals have probably been intensively selected for. This in turn may cause coyote populations to resist control practices that previously were effective. In addition, the possibility of social facilitation and learning may be altered or reduced. Coyotes, like many mammals, learn to habitually use certain prey or habitats from other individuals in the population, especially from older adults in their social group (if they have one). Coyotes, already a highly social and adaptable species, are held in a younger colonizing state when they are exploited, and learned or traditional behaviors may be lost. Individuals are therefore more susceptible to learning novel prey sources or trying out novel habitat types, and are frequently associated with conflicts such as livestock predation.

There are many questions to be answered such as, "How will coyote populations respond once predator reduction or control programs are terminated?" or "Are there other management alternatives, both lethal and non-lethal, that may be effective in reducing predation on domestic livestock"? "How do economics figure into management options"? This letter and scientific opinion only addresses the narrow, but important topic of the impacts of human-caused reduction or 'control' on coyote demographic parameters. We see little, if any, evidence to justify control practices on an ecological basis. This letter also addresses a long-held belief that human control of coyote populations are 'necessary', similar to 'mowing a lawn' to keep it from growing out of control. This belief has no scientific basis whatsoever. Even research conducted by Wildlife Services reports a variety of factors that keeps the lawn from growing. Their research repeatedly concludes that the primary means of population limitation is territoriality itself, which imposes an upper limit on density (or lawn height). Paradoxically the prevalent use of lethal control by Wildlife Services opens up a 'Pandora's box' of behavioral and demographic responses that negate any long-term effectiveness of control. The predominant responses of coyote populations to lethal control efforts are to: (1) increase the number of pups produced (recruitment), (2) increase immigration into the conflict area, and (3) increase behaviors that further exacerbate the conflict. Collectively, this results in higher predation rates on domestic livestock and wild ungulates.

Coyotes are still products of their evolutionary past. Biological, economical, and ecological evaluation of control practices should be a requirement undertaken before any public or private effort to reduce losses due to coyotes or any other predator. In conclusion, it is my opinion based on decades of field research that the common practice of reducing adult coyote populations on western rangelands is most likely ineffective and likely causes an increase the number of lambs, fawns, and calves killed by coyotes.

A Summary of the Effects of Exploitation on Predator Populations

The 20 responses listed below are divided into four general categories: (1) demographic compensation, (2) behavioral response, (3) changes in culture/society, and (4) ecosystem impacts. How many of these occur—and their individual magnitudes—will vary by species, the severity and type of control action taken, habitat, season, prey availability, and presence of competing carnivores in the target area. Interactions between the 20 responses listed below can be unpredictable; however, scientific findings and biological common sense both indicate that they 'amplify' in a manner that renders indiscriminate killing ineffective and results in a multitude of detrimental effects on individuals, species populations, and the entire predator-prey ecosystem.

Demographic Compensation: (this is a particularly strong response for coyote populations because the primary reason they kill ungulate neonates, both domestic and wild, is to feed fast-growing pups)

- Breeding adults produce more pups when there is direct reduction in territorial pack size. There is a weak to negligible effect on litter size at birth; however, the compensatory response of litter survival is remarkable. For example, prior to wolf restoration, adult coyote mortality averaged only 9%, pack size was 6, and litter survival was 28%. After wolf restoration, adult coyote mortality increased to 30% to 50%, pack size fell to 3, and coyote pup survival abruptly rose to 78%—a nearly three-fold increase. Analysis from 20+ field studies indicated a similar response to human exploitation.
- Immigration of breeding adults into the exploited area to fill vacant territories and find available mates. This response can be immediate. I have documented successful coyote litters in territories where the pregnant female was killed one month earlier (ascension by

a pregnant beta female—Wildlife Service's own research documents this phenomenon—nearly all non-alpha females are pregnant on an annual basis).

- A higher percentage of females breed and produce pups. Two litters per territory can also occur with abundant/available prey.
- The average age of reproductive females is lowered, eliminating older, less productive alpha females. First-time breeders (young alphas) have higher pup survival than older breeding pairs.
- Increased natal philopatry—yearlings and young betas tend to forego dispersal and continue to reside in the exploited area.
- Regardless of the level of exploitation, the number of breeding pairs in a target area is consistent from year to year unless 70% or more of the coyote population is removed annually. This level of control is extremely difficult and costly to achieve let alone document.

Behavioral Responses:

- Lower pack size results in selection of larger prey items (e.g., ungulate neonates) over more numerous small prey items (e.g., rodents). This is particularly detrimental to livestock when alternate prey abundance is low which is often due to overgrazing practices.
- Adjust vocal communications—less vocal around humans.
- Activity cycles—more nocturnal and less diurnal.
- Denning behavior (guarding and location)—less susceptible to enemies.
- Avoidance of novel stimuli including control techniques. Perceived avoidance of sustained control activities.

Changes in the Culture/Society:

- Increases in information sharing within and between new territorial pack members; this leads to increased exposure to novel prey (livestock).
- Because there is a strong shift to fewer subordinates—betas are immediately recruited to alpha breeding status—livestock-killing alpha adults are predominant in the population structure.
- Killing the alpha male results in immediate replacement or the remaining pack breaks apart and disperses to form breeding pairs elsewhere.
- Indiscriminate control methods have accelerated and amplified selection pressures to perpetuate a 'dispersal genotype' adapted to rapidly colonize and successfully reproduce. Remember that during the predator eradication era (approximately 1860's to 1960's), large carnivore populations declined substantially (with regional extirpation) while coyotes tripled their abundance and distribution across North America.
- Their cultural evolution likely interacts with their biological evolution to further accelerate and amplify selection pressures.

Ecological Impacts:

- Mesopredator release: Decrease in apex predator populations reduces the competition and/or intraspecific killing rates with other predators or mesopredators (e.g., foxes, raccoons, skunks, feral cats, etc.). This causes an increase in their abundance (i.e., release), which in turn, can have detrimental effects on other species (e.g., ground-nesters, songbirds, amphibians, and rodents) and other unintended 'ripple' effects or trophic cascades.
- Loss of ecosystem services: alleviation of control pressures on prey populations (e.g., rodents, large herbivores) can lead to vegetation changes.
- Loss of ecosystem services: Disruption and increase of disease spread.
- Loss of ecosystem services: Loss of subsidies to scavengers (e.g., wolves provides food for many other species).

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